CHROMOSOME NUMBERS IN LUPINUS

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The genus *Lupinus*, a member of the sub-family Papilionoideæ of the Leguminosæ, is a group of world-wide distribution with population centers in western United States, Europe, and South America. The present cytological study was undertaken in conjunction with a taxonomic revision of the perennial lupines of North America (Phillips, 1955) in which sixteen species and sixteen infra-specific taxa are recognized. Chromosome numbers are listed below for twenty-six of these taxa.

Figs. 1–5. *Lupinus* meiosis and mitosis: *1, L. laxiflorus* var. *laxiflorus,* M_I, n=24; *2, L. sulphureus* subsp. *sulphureus,* Diak., n—24; *3, L. saxosus,* late Diak., n=48; *4, L. humicola,* T_I, n=24; *5, L. sericeus* subsp. *sericeus,* c-mitotic metaphase, n=24. The camera lucida drawings of the chromosomes were made at a magnification of 1940 and reduced to 970.

The chromosome number determinations were made either at diakinesis or metaphase I of microsporogenesis or metaphase of root mitosis. The meiotic material was fixed in Carnoy III (3 parts ethanol, 4 parts chloroform, and 1 part acetic acid) and smeared in aceto-carmine or propionocarmine. Root tips were treated in oxyquinoline according to Tjio and Levan (1950) and smeared in aceto-orcein. Pollen fertility analyses were made with cotton blue lacto-phenol.

The present study on the perennial lupines and several previous reports on the chromosome numbers of Old World species (Kawakami, 1930; Savchenko, 1936; Tuschnjakowa, 1935; and Maude, 1940) make it apparent that the basic number of the genus is 12. Diploid (n=12) and tetraploid (n=24) species as well as several taxa that deviate from the basic number (n=21, 25, 26) are cited for Europe and Africa. Of the

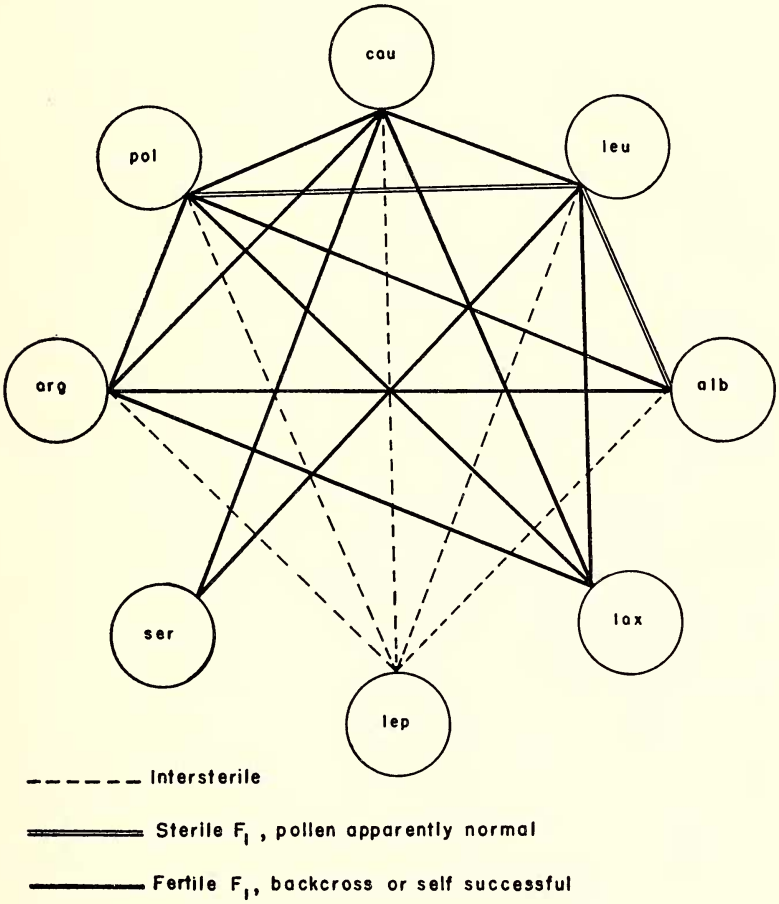

FIG. 6. Breeding behavior of eight species of *Lupinus* of the Northwestern United States. All taxa n=24: alb. = *L. albicaulis;* arg. = *L. argenteus* subsp. *argenteus;* cau. = *L. caudatus* subsp. *caudatus;* lax. = *L. laxiflorus* var. *laxiflorus;* lep. = *L. lepidus* subsp. *lepidus;* leu. = *L. leucophyllus;* pol. = *L. polyphyllus* var. *polyphyllus;* ser. = *L. sericeus* subsp. *sericeus.*

twenty-six North American taxa examined cytologically twenty are tetraploid, two are octaploid (n=48), and four are both tetraploid and octaploid. The octaploid chromosome level has been heretofore unreported for the genus.

In none of the four taxa which contain two chromosome "races" is this difference in chromosome number correlated with morphological dissimilarities. Apparently the genetic isolation created by chromosome doubling in these taxa has not been operative long enough to permit divergence into morphologically definitive types. In a few instances populations of octaploids are somewhat unique as compared with related tetraploids, but these unique individuals or populations fall within the variation pattern of the taxon as a whole and cannot justifiably be given specific or infraspecific recognition.

Figure 6 presents a summary of a hybridization study involving eight tetraploid species native to Northwestern United States. It can be seen that all of the interspecific crosses were successful except those crosses involving *L. lepidus*. The F_1 hybrids exhibited nearly regular meioses (occasionally lagging chromosomes were seen at metaphase I), and a fairly high degree of pollen fertility (75–85 per cent). Attempted crosses of *L. lepidus* × *L. argenteus* and *L. lepidus* × *L. leucophyllus* resulted in the production of normal seed pods containing aborted ovules. Since no such stimulatory effect on pod development was observed with other crosses involving *L. lepidus*, this is interpreted to mean that, of the species studied, *L. lepidus* is most closely related to *L. argenteus* and *L. leucophyllus*.

The apparent lack of genetic barriers between these species, demonstrable under experimental conditions, is also evident in the field where hybrid individuals often result wherever two or more species are sympatric. Occasionally hybrids and introgressants in such a sympatric association will completely blur species boundaries, but more often the discernible intermediates are relatively few in number. Presumably, the plants of hybrid nature are not able to compete with parental species except where there are uncolonized habitats available for which they are better adapted than the parents.

The low level of genetic differentiation between the species utilized in this study supplies a reasonable explanation for the extreme variability within species and for the overlapping variation pattern between many species. Species that can exchange genetic material readily are bound to be variable and difficult to separate taxonomically. Hence *Lupinus* has become known to taxonomists as a "difficult" genus.

For some of the wide-ranging taxa (*L. laxiflorus* var. *laxiflorus*, *L. sericeus* subsp. *sericeus*, *L. polyphyllus* var. *polyphyllus*) the citations listed below constitute only a portion of the collections counted. In these taxa the collections cited have been selected to reflect the geographical range from which cytological analysis has been made. The collections listed below are deposited in the Washington State College Herbarium.

Taxon	Chromosome Number (n)	Collection
L. albicaulis	24	Seattle, King County, Washington, *Phillips 690*.
	24	5 miles south of Kelso, Cowlitz County, Washington, *Phillips 667*.
	24	Mollala, Clackamas County, Oregon, *Phillips 720*.
L. argenteus subsp. *argenteus*	24	5 miles west of Bridgeport, Baker County, Oregon, *Phillips 634*.
	24	Pierce, Clearwater County, Idaho, *Phillips 786*.
	24	Alberton, Missoula County, Montana, *Phillips 860*.
	24	10 miles east of Livingston, Park County, Montana, *Phillips 855*.
	24	12 miles west of Custer, Custer County, South Dakota, *Phillips 846*.
subsp. *parviflorus*	24	5 miles east of Soda Springs, Bear Lake County, Idaho, *Phillips 792*.
L. caudatus	24	Baker, Baker County, Oregon, *Phillips 635*.
subsp. *caudatus*	24	2 miles south of Madras, Jefferson County, Oregon, *Phillips 627*.
subsp. *argophyllus*	48	Monticello, Summit County, Utah, *J. Nishitani 7–1952*.
L. humicola	24	Leavenworth, Chelan County, Washington, *Phillips 733*.
	24	Near Manhattan, Broadwater County, Montana, *Phillips 858*.
	24	Acme, Sheridan County, Wyoming, *Phillips 836*
L. laxiflorus var. *laxiflorus*	24	Omak, Okanagan County, Washington, *Phillips 606*.
	24	Winton, Chelan County, Washington, *Phillips 728*.
	24	Selah, Yakima County, Washington, *Phillips 627*.
	24	Near Mount Hood, Hood River County, Oregon, *Phillips 621*.
	24	6 miles east of Sisters, Deschutes County, Oregon, *Phillips 707*.
	24	2 miles south of White Bird, Idaho County, Idaho, *Phillips 800*.
	24	12 miles north of Boise, Ada County, Idaho, *Phillips 803*.
	48	Lyle, Klickitat County, Washington, *Phillips 683*.
	48	Underwood, Skamania County, Washington, *Phillips 610*.
var. *pseudoparviflorus*	24	Near Priest River, Bonner County, Idaho, *Phillips 852*.

Taxon	Chromosome Number (n)	Collection
	24	St. Regis, Mineral County, Montana, *Phillips 865.*
L. lepidus subsp. *lepidus*	24	Spanaway, Pierce County, Washington, *Phillips 582.*
	24	3 miles south of Goldendale, Klickitat County, Washington, *Phillips 612.*
	24	Dayville, Grant County, Oregon, *Phillips 630.*
	24	Near Ukiah, Umatilla County, Oregon, *Phillips 715.*
	24	6 miles north of Modoc Point, Klamath County, Oregon, *Phillips 892.*
subsp. *lyallii*	24	Toll Gate, Umatilla County, Oregon, *Phillips 699.*
L. leucophyllus	24	Near Thorpe, Kittitas County, Washington, *Phillips 642.*
	24	2 miles north of Spangle, Spokane County, Washington, *Phillips 876.*
	24	Goldendale, Klickitat County, Washington, *Phillips 658.*
	24	Near Pullman, Whitman County, Washington, *Phillips 842.*
	24	La Grand, Umatilla County, Oregon, *Phillips 636.*
	24	Dixie, Baker County, Oregon, *Phillips 633.*
	24	5 miles north of Boise, Ada County, Idaho, *Phillips 804.*
	48	Near Goldendale, Klickitat County, Washington, *Phillips 678.*
	48	Wapato, Yakima County, Washington, *Phillips 620.*
L. littoralis	24	Hecata Beach, Lane County, Oregon, *Kruckeberg 3315.*
L. polyphyllus var. *polyphyllus*	24	Montsanto, Thurston County, Washington, *Phillips 596.*
	24	Mission Peak, Kittitas County, Washington, *Phillips 676.*
	24	2 miles east of Livingston, Park County, Montana, *Phillips 851.*
	24	Oswego, Clackamas County, Oregon, *Phillips 646.*
	24	Near Viola, Garfield County, Washington, *Phillips 902.*
var. *prunophilus*	24	Wawawai, Whitman County, Washington, *Phillips 869.*
L. perennis subsp. *perennis*	24	4 miles east of Plymouth, Marshall County, Indiana, *Phillips 822.*

Taxon	Chromosome Number (n)	Collection
	24	Amboy, Lee County, Illinois, *Phillips 815.*
	24	Near Hanover, Lebanon County, Pennsylvania, *Phillips 830.*
subsp. *latifolius*	24	Mt. Rainier, Pierce County, Washington, *Phillips 613.*
	48	Zigzag, Clackamas County, Oregon, *Phillips 628.*
subsp. *plattensis*	24	5 miles east of Kimball, Kimball County, Nebraska, *Phillips 809.*
L. saxosus	48	10 miles south of Liberty, Kittitas County, Washington, *Phillips 689.*
L. sericeus subsp. *sericeus*	24	Maryhill, Klickitat County, Washington, *Phillips 687.*
	24	Big Timber, Sweetgrass County, Montana, *Phillips 851.*
	24	Gillette, Campbell County, Wyoming, *Phillips 849.*
	24	Orofino, Clearwater County, Idaho, *Phillips 890.*
subsp. *asotinensis*	24	Indian, Whitman County, Washington, *Phillips 792.*
	24	10 miles west of Clarkston, Asotin County, Washington, *Phillips 811.*
subsp. *sabinii*	24	Elgin, Union County, Oregon, *Phillips 736.*
L. suksdorfii	48	Glenwood, Klickitat County, Washington, *Phillips 679.*
L. sulphureus subsp. *sulphureus*	24	Kooskooskie, Walla Walla County, Washington, *Phillips 696.*
	24	2 miles east of Viola, Garfield County, Washington, *Phillips 903.*
subsp. *kincaidii*	24	Silverton, Polk County, Oregon, *Phillips 721.*
subsp. *subsaccatus*	24	10 miles south of Wenatchee, Kittitas County, Washington, *Phillips 746.*
	24	Cle Elum, Kittitas County, Washington, *Phillips 688.*
	48	Ellensberg, Kittitas County, Washington, *Phillips 674.*
	48	6 miles south of Coulee City, Grant County, Washington, *Phillips 882.*
subsp. *whithamii*	24	Butch Creek, Pend Oreille County, Washington, *Rumely* & *Phillips 453.*
	24	Near Nordman, Bonner County, Idaho, *Rumely* & *Phillips 455.*
	24	West shore of Priest Lake, Bonner County, Idaho, *Rumely* & *Phillips 456.*

Summary

Chromosome number determinations for 26 taxa of North America indicate twenty of these to be tetraploid (n=24), two to be octaploid (n=48), and four taxa to be both tetraploid and octaploid.

A hybridization study involving eight species of Northwest United States shows genetic incompatibility barriers to be poorly developed between these species, thus supplying a possible reason for the overlapping patterns of morphological variation found in the genus *Lupinus*.

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Mr. Jerome D. Laudermilk, who passed away in January, 1956, was a general scientist. The originality of his inquisitive mind impressed those who knew him well. He read widely and probed deeply as he read. Characteristically he was not satisfied to accept Leeuwenhoek's account of his microscope until he had ground lenses and made a microscope of his own exactly according to Leeuwenhoek's formula. The structure of ancient weapons was a special field of research, and he lectured and demonstrated his models publicly and for the Pomona College Department of Military Science and Tactics. He was interested so deeply in the operations of those who deal in the occult that at one time he was kidnapped, taken to an obscure house, and convinced that his life would be longer if he did not write on the subject.

Jerry Laudermilk was a graduate of Kansas State College of Pharmacy, and he served in the United States Army in World War I. Being in ill health he spent several years in the desert near Wickenberg, Arizona, where he developed a deep interest in and knowledge of desert vegetation. He came to southern California thirty-five years ago, and he lived for the last thirty years in Claremont, where he was Research Associate in Geochemistry and Paleobotany at Pomona College. There, in association with Dr. Philip A. Munz, he investigated the food habits of extinct giant sloths by study of the dung of the animals in the caves they inhabited in the deserts near the Colorado River. This has provided knowledge of the past vegetation of the area.